

THE BASES OF ANGIOSPERM PHYLOGENY: ULTRASTRUCTURE^{1,2}

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ABSTRACT

A classification of sieve-element plastids by their major accumulation of ergastic products (protein or starch) into P-type and S-type, based on the ultrastructural research of some 500 species, provides systematists with a new micromorphological character to be used for a reconsideration of the outline of some of the higher taxa in the Takhtajan system of Magnoliophyta. Plastid types are listed for families and orders of Liliopsida and the first four subclasses of Magnoliopsida. Of these, Magnoliidae and Caryophyllidae are discussed in greater detail. It is demonstrated that sieve-element plastids can contribute relevant data to the rearrangement of at least some of the taxa in question. In addition some remarks are made on possible phylogenetic trends among the different plastid types.

Ultrastructure is a rather new field contributing to plant systematics. Despite the comparatively short time which has passed since its introduction, various techniques have already been used very successfully to contribute valuable micromorphological characters to distinctive taxonomic problems.

Cole & Behnke (1975) gave a short synopsis of new characters derived from comparative studies with the electron microscope, and a detailed evaluation of their application to plant systematics is being prepared (Behnke & Cole, in preparation). The data presented so far clearly demonstrate that, unlike the situation with lower plants, ultrastructural characters in higher plant systematics are largely confined to results achieved with the scanning electron microscope. With its potentiality to disclose new dimensions of plant surface the scanning electron microscope greatly extends our knowledge of morphological differences. In all of the recent attempts to come to a natural and phylogenetic system of higher plants, and of Magnoliophyta (Angiospermae) in particular, morphological information still ranks very high. Consequently, the scanning electron microscope seems more adequate to systematists and has more readily been accepted by them than other ultrastructural tools such as the transmission electron microscope and the freeze etching device. Thus the former failure of ultrastructural research to contribute reliable characters to magnoliophytan systematics may in part be due to its restriction to the cellular and subcellular level of the transmission electron microscope. There are two major reasons which explain why, for a long period, transmission electron microscopy did not even provide minor characters of taxonomic significance to the classification of Magnoliophyta: (1) within any given tissue, cell organelles are considered to be uniform; and (2), the distribution

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in Magnoliophyta of the relatively few different species that have been investigated with respect to a certain tissue is random.

It therefore was an exciting experience when we first became aware of the applicability of ultrastructural data of sieve-element plastids to taxonomic problems (Behnke, 1967, 1969a). Continued research on a gradually expanding number of species and higher taxa supported and substantiated our concept of the new micromorphological character in seed plant systematics. Application and reliability of sieve-element plastid ultrastructure to systematic and phylogenetic questions in Magnoliophyta is presented in this contribution to the symposium.

Since the present discussion will in general only descend to the family level, it may be convenient to refer to the detailed listing of species and references given in Behnke (1972) and to an additional list kept up-to-date by the author. The combined lists include ultrastructural data on more than 500 species.

TECHNIQUE

Sieve elements of any part of a plant can be used for a study of their plastids. Young stem parts are preferred in the majority of species investigated because of their easier handling, but roots, leaves, and flower stalks, which were used in some species, give equivalent results. In general, longitudinal hand sections of the appropriate plant part containing vascular bundles are fixed in a formaldehyde-glutaraldehyde mixture followed by treatment with osmic acid (for details see Behnke, 1975a). After dehydration in acetone, sections are recut into small phloem-containing pieces just before polymerization in epoxy resins. Trimming of the polymerized material proceeds with the control of a binocular microscope so as to obtain a top plane with less than 100 μm side length and with sieve elements in its center. Ultrathin sections (thickness about 50 nm), cut with glass or diamond knives, are viewed and photographed with a transmission electron microscope at varying magnifications (5–40,000 $\times$ in general). Determination of accumulation products within sieve-element plastids is done by specific staining reactions in light microscopic monitor sections, by enzymatic digestion within the ultrathin section (Behnke, 1967, 1975a), and occasionally by comparing their staining response to fixatives and contrast-enhancing material under the electron microscope with those of well-known examples.

PRINCIPAL CHARACTERS OF PHYLOGENETIC SIGNIFICANCE

Plastids are among the normal and continuous constituents of each living plant cell. Though there are different classes of plastids within different cells and tissues—e.g., chloroplasts, chromoplasts, or leucoplasts—a plastid can only be derived from a plastid of either the same or another class. Furthermore, it should be stressed at the very beginning that throughout the following discussion we will deal exclusively with *sieve-element* plastids. There are other plastids or other organelles that show structural differences on the inter- or intraspecies levels, but sieve-element plastids presently are the only organelle type that can be used as a structural character for considerations of the classification of higher taxonomic levels throughout Spermatophyta.

Sieve-element plastids are to be classified as leucoplasts, the class of non-

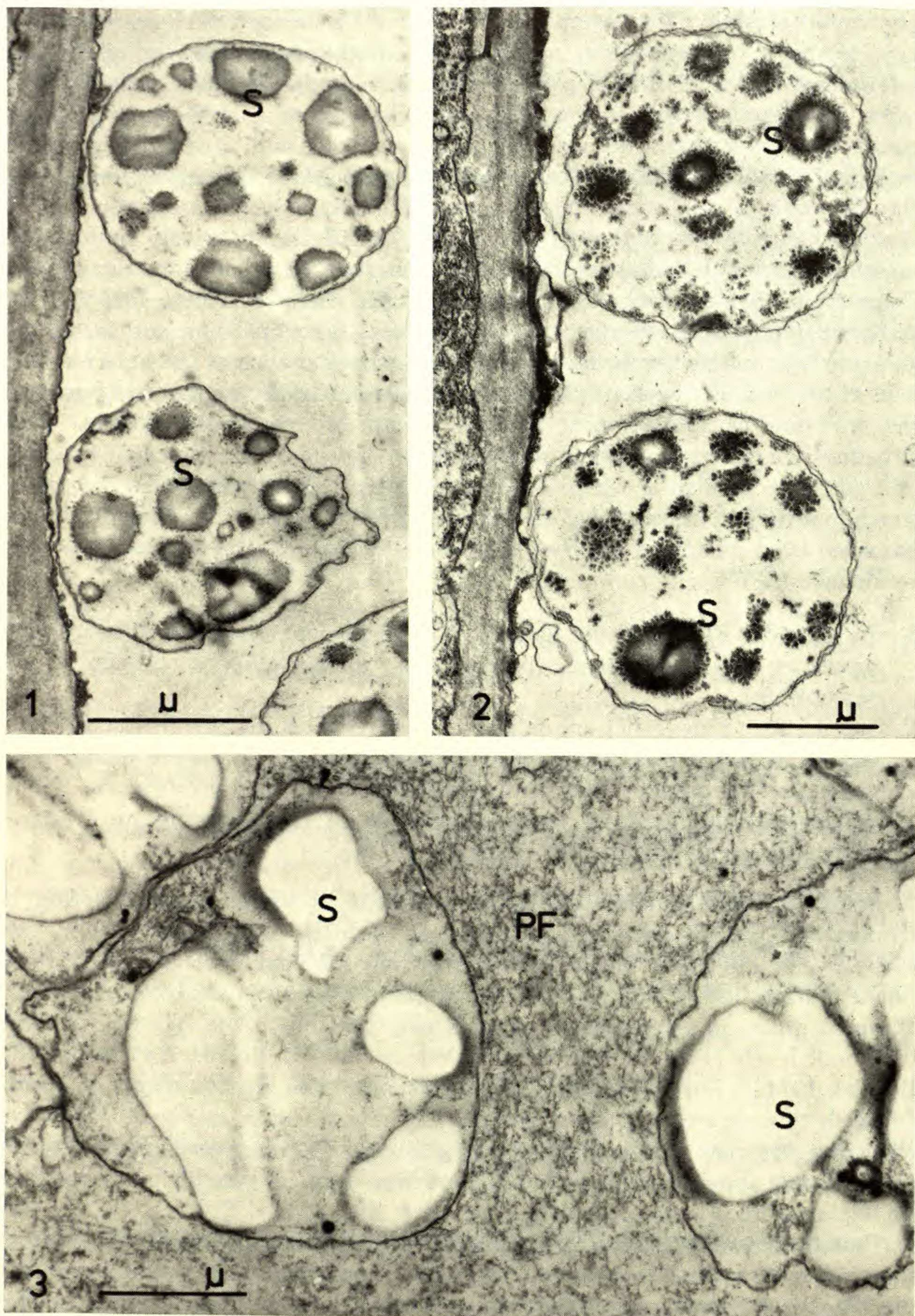
pigmented plastids. They are often called 'juvenile leucoplasts' because of their low degree of differentiation and deviation from proplastids, the plastids of meristematic cells. Plastids of phloem cells adjoining the sieve elements may have quite a different structure, e.g., there are chloroplasts in phloem-parenchyma cells. A common proplastid, elongated and amoeboid, with a dense inner matrix including some thylakoids, and surrounded by a double envelope, is the source of the different types of sieve-element plastids. During the differentiation of the sieve elements these proplastids show a gradual decline in matrix contents, an associated accumulation of ergastic storage material, and a transformation of their shape from oblong-amoeboid to spherical forms (Behnke, 1969a, 1969b). The differentiated plastids survive all structural and functional changes within the sieve element and do not disintegrate before final obliteration of the sieve element, e.g., at the end of a season. Therefore, taxonomic characters that are based on the structure of sieve-element plastids should be reasonably reliable. Such structural characters considered of taxonomic importance are the major products of ergastic accumulation, viz., sieve-element starch and protein. The amount of starch and protein, respectively, that is accumulated in the sieve-element plastids has been used as an aid for the artificial distinction of plastid types proposed by Behnke (1971a):

S-type plastids (Figs. 1–3) are defined as sieve-element plastids that accumulate starch as the main storage product (an accumulation of protein is not perceptible).

P-type plastids (Figs. 4–17) are defined as sieve-element plastids that accumulate protein as single product or in addition to starch. The ultrastructural morphology of the protein inclusions (their sizes, forms, and arrangement within the plastid) are used for a characterization of taxon-specific sub-types of protein accumulating plastids (Behnke, 1975a).

Starch in sieve-element plastids is deposited as single grains differing in number, size, shape, and stainability as seen with the electron microscope, and each species obviously has its own genetically defined type of starch grain (Badenhuizen, 1973), Figs. 1–3. There are some indications that the morphology of starch grains in sieve-element plastids may turn out to be specific for some taxonomic levels (Palevitz, unpublished data on Fabales; Behnke & Paliwal, 1973; Behnke, 1974a), but investigations at the present time are too scanty to firmly establish this. Moreover, the structural changes of starch grains during sieve-element aging may also play an important role. The chemical composition of sieve-element starch is apparently different from ordinary starch as demonstrated by sequential enzymatic digestion (Palevitz & Newcomb, 1970).

Protein accumulations in sieve-element plastids are present in the form of filaments or crystalline inclusion bodies, both being arranged in various ways, but the latter is in many cases presumably derived from the former (Figs. 4–17). Some forms of protein inclusions are typically restricted to some taxa of different taxonomic levels and can be defined as sub-types of the P-type plastids. These plastid inclusions have been identified as protein by enzymatic digestion with proteases (Behnke, 1975a), by their specific staining response against mercuric



FIGURES 1-3. Sieve-element plastids of the S-type with many starch grains (S).—1. *Ocotea foetens* (Lauraceae); $\times 22,000$.—2. *Cocculus trilobus* (Menispermaceae); $\times 18,000$.—3. *Cassytha filiformis* (Lauraceae); $\times 20,000$. PF = protein filaments within sieve-element protoplasm.

bromphenol blue, and by their reaction in KMnO_4 fixatives (for references see Behnke, 1972).

COMPARATIVE ULTRASTRUCTURE OF SIEVE-ELEMENT PLASTIDS AND THE
TAKHTAJAN-CRONQUIST SYSTEM OF CLASSIFICATION OF
MAGNOLIOPHYTA (ANGIOSPERMS)⁴

CLASS LEVEL: MAGNOLIOPSIDA (DICOTYLEDONS) VERSUS
LILIOPSIDA (MONOCOTYLEDONS)

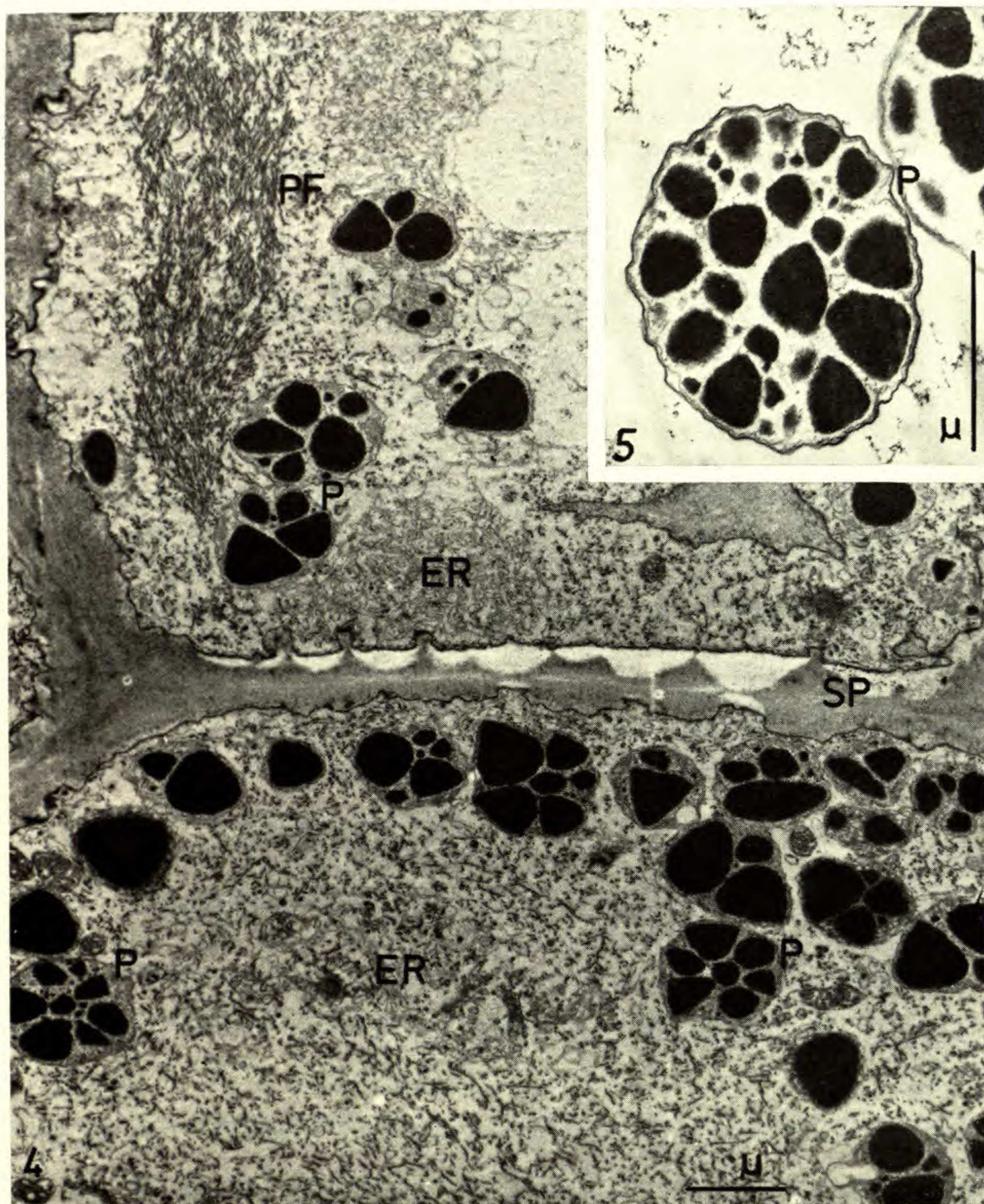
Within Liliopsida sieve-element plastids have a highly uniform structure (Figs. 4–5), as far as can be determined from the diverse taxa investigated. Among Magnoliopsida, on the other hand, all of the different P- and S-type plastids currently known are recorded in the sieve elements of one taxon or another, some subtypes being closely restricted to individual taxa. Concerning the structure of the sieve-element plastids, only one investigation in the Magnoliopsida has come to our attention that shows an obvious homology to specific P-type plastids in Liliopsida: *Asarum* (four species investigated) of the Aristolochiaceae has the same cuneate protein crystalloids (subtype P:vcC)⁵ with similar reactions to proteinase digestion and presumably the same pattern of arrangement as shown for Liliopsida (Fig. 13; Behnke, 1971b, 1975a). Unlike plastid types of Magnoliopsida, a relation between the P-type specific to Liliopsida and sieve-elements of Gymnospermae could not be found. Hence judging from the present available data on ultrastructure of sieve-element plastids, Liliopsida are a comparatively uniform and settled taxonomic group.

SUBCLASS LEVEL

Magnoliopsida.—Our knowledge concerning the ultrastructure of sieve-element plastids of Magnoliopsida presently extends to more than 400 species belonging to some 110 families of 52 of the 73 orders. Nearly 200 species contain P-type plastids, but they come from only 31 families of 9 orders. However, it should be mentioned that intensive research has only been done with the first four subclasses (Magnoliidae through Caryophyllidae). Two of them (Ranunculidae and Hamamelididae) almost exclusively contain S-type plastids, Ranunculidae being the subclass of Magnoliopsida with the highest degree of homogeneity (100% S-type according to present information). Caryophyllidae and Magnoliidae show a large diversity in distribution of plastid-types and attain the maximum mixture of plastid-types in Magnoliidae. There is not much that can be said about supporting or opposing the composition of the subclasses as defined by Takhtajan (1973). The occurrence of only S-type plastids in Ranunculidae and Hamamelididae emphasizes the uniformity of these subclasses. But we can not easily make a distinction between them since ultrastructure so far does not provide criteria for a subdivision of S-type plastids.

⁴ The taxa used down to the family level, and their systematic arrangement follow the latest version of Takhtajan's (1973) system of flowering plants.

⁵ Classification of subtypes after Behnke (1975a).



FIGURES 4–5. P-type plastids (P) in Liliopsida (subtype P:vcC).—4. Two sieve elements of *Tradescantia albiflora* (Commelinaceae) separated by a sieve plate (SP); $\times 12,000$. Many P-type plastids with cuneate crystalloids occur within the protoplasm. PF = characteristic protein filaments of sieve-element protoplasm; ER = endoplasmic reticulum.—5. P-type plastid with cuneate crystalloids in characteristic pattern in sieve element of *Dracaena hookeriana* (Liliaceae); $\times 25,000$.

Caryophyllidae, as here delimited, apparently are not very homogeneous. There is an outstanding difference between Caryophyllales—reported to contain specific P-type plastids—and the remaining orders that have S-type plastids.

The marked mixture of taxa with S-type and different subtypes of P-type

TABLE 1. P-type sieve-element plastids (subtype P:cvC [S]) in orders of Liliopsida.^a
(Figures following the orders represent the number of investigated families/genera/species.)

74. Alismales	3/3/3	84. Bromeliales	1/3/3
75. Hydrocharitales	1/1/1	85. Commelinales	1/4/4
76. Najadales	1/1/1	86. Eriocaulales	1/1/1
77. Triuridales	—	87. Restionales	3/3/3
78. Liliales	9/21/26	88. Poales	1/9/10
79. Iridales	1/1/1	89. Arecales	1/11/19
80. Zingiberales	4/4/5	90. Cyclanthales	1/1/1
81. Orchidales	1/5/5	91. Arales	2/4/4
82. Juncals	1/2/2	92. Pandanales	1/1/1
83. Cyperales	1/1/1	93. Typhales	2/2/2
TOTALS		36/78/93	

^a For references see Behnke (1972).

plastids that has been shown to occur in Magnoliidae is probably due to the basal position that this subclass is thought to occupy in the evolution of the flowering plants.

Liliopsida.—Among the 93 investigated species from the four subclasses there is high conformity in the structure of their sieve-element plastids (Table 1). The specific pattern of P-type plastids (subtype P:vcC[S]) in Liliopsida includes cuneate protein crystalloids that are most prominently oriented toward the center of the plastid matrix (Figs. 4–5). Sizes and number of crystalloids vary, as well as sizes of the plastids. Accumulation of starch in addition to that of protein is recorded for some families, including all of those looked at in Zingiberales and Arales. Although there are particular patterns that are common only to Zingiberales (see Behnke, 1972), the deposition of starch in sieve-element plastids of Liliopsida does not appear to have an important relation to taxonomic considerations. For example, there are members of the *Dioscorea* genus that accumulate starch and others that do not.

Investigated species of the order Poales (10) display a character that is probably order-specific: in addition to the class-specific cuneate crystalloid, there is a second protein inclusion composed of tubular subunits.

ORDINAL-INTERFAMILIAL LEVEL

Magnoliidae.—Species of 19 of the 29 families from all orders were investigated (Table 2). The uniformity of sieve-element plastid types for families is rather high (8 with P-type, 10 with S-type, only one with both), but among the orders, there is more diversity. Magnoliales and Laurales are quite well balanced between P- and S-type containing families, while Piperales and Nymphaeales have S-type, and Aristolochiales only P-type plastids. Neither starch nor protein could be detected in sieve-element plastids of Rafflesiales. It may be important to stress that the P-type order Aristolochiales is often looked upon as specifically related to Annonaceae—as for example, based on phytochemical investigations (Hegnauer, 1960)—which is among those families of Magnoliales that contain P-type plastids exclusively. The specific modification of sieve-element plastids in

TABLE 2. Sieve-element plastids in Magnoliidae.^a (Figures following the families represent the number of investigated genera/species; P = P-type, S = S-type plastids.)

Order 1: Magnoliales		Order 3: Piperales	
Magnoliaceae	S 2/4	Saururaceae	S 2/2
Eupomatiaceae	P 1/1	Piperaceae	S 2/5
Annonaceae	P 5/9		
Canellaceae	P 1/1	Order 4: Aristolochiales	
Myristicaceae	P 1/1	Aristolochiaceae	P 2/13
Winteraceae	S 2/2		
Order 2: Laurales		Order 5: Rafflesiales	
Austrobaileyaceae	S 1/1	Rafflesiaceae	2/2 ^c
Monimiaceae	P 4/5		
Hernandiaceae	P 2/2 ^b	Order 6: Nymphaeales	
Chloranthaceae	S 1/1	Cabombaceae	S 1/1
Calycanthaceae	P 2/4	Nymphaeaceae	S 2/2
Lauraceae	P 1/2	Barclayaceae	S 1/1
	S 7/8		
TOTALS P 19/38; S 21/27; 212 ^c			

^a All investigations by the author.
^b Investigations include *Sparatthantelium* (formerly placed in Gyrocarpaceae).
^c Insufficient material, neither starch nor protein detected in sieve-element plastids.

Aristolochia (Fig. 11) almost equals that of *Annona* (P:lpC.S; Fig. 6), while *Asarum* has exactly the same type as monocotyledons (P:vcC; compare Fig. 5 and Fig. 13). The detection of P-type plastids in sieve-elements of Eupomatiaceae, Annonaceae, Canellaceae (Fig. 7), and Myristicaceae, although all with different subtypes, parallels chromosomal data reported and used for evolutionary considerations by Ehrendorfer et al. (1968).

In Laurales Ehrendorfer et al. (1968) assign the phylogenetic basis to Monimiaceae to which are connected (1) Calycanthaceae and (2) a more advanced group: Lauraceae—Hernandiaceae(–Gyrocarpaceae). It is of interest to state that these families are also connected by the formation of P-type sieve-element plastids (for different modifications see Figs. 8–10), while other groups contain S-type plastids (see Table 2). In Lauraceae, however, only *Laurus* was found to have P-type plastids.

Cronquist (1968), while discussing the different characters in favor of an intermediate position of Eupomatiaceae, in his synoptical arrangement of families associates this family to his lauraceous cluster. The P:vpC.S modification of its plastids is very like that of Monimiaceae (Fig. 8) and would favor a placement within Laurales.

Ranunculidae.—There is a 100% representation of S-type plastids among the 13 families investigated from the total of 16 families recorded by Takhtajan

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FIGURES 6–13. P-type sieve-element plastids of Magnoliidae. Diversity of subtypes is shown for three orders. For taxon-specific pattern, see individual figures.—6–7. Magnoliales.—8–10, 12. Laurales.—11, 13. Aristolochiales. b = bundle; C = crystalloid; c = cuneate; F = filaments; g = globular; i = irregular; l = large sized; m = minor sized; P = P-type; p = polygonal; v = variable.

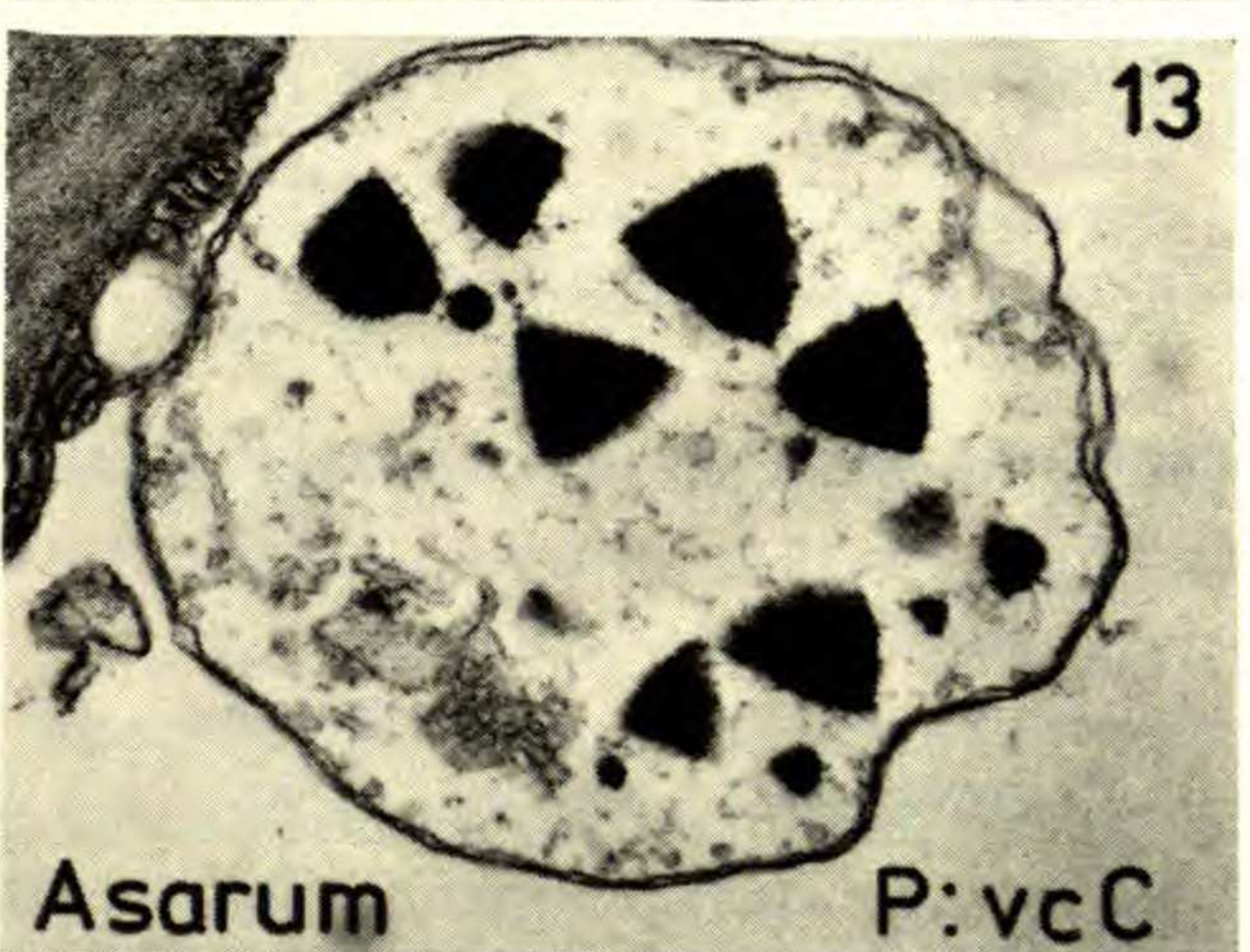
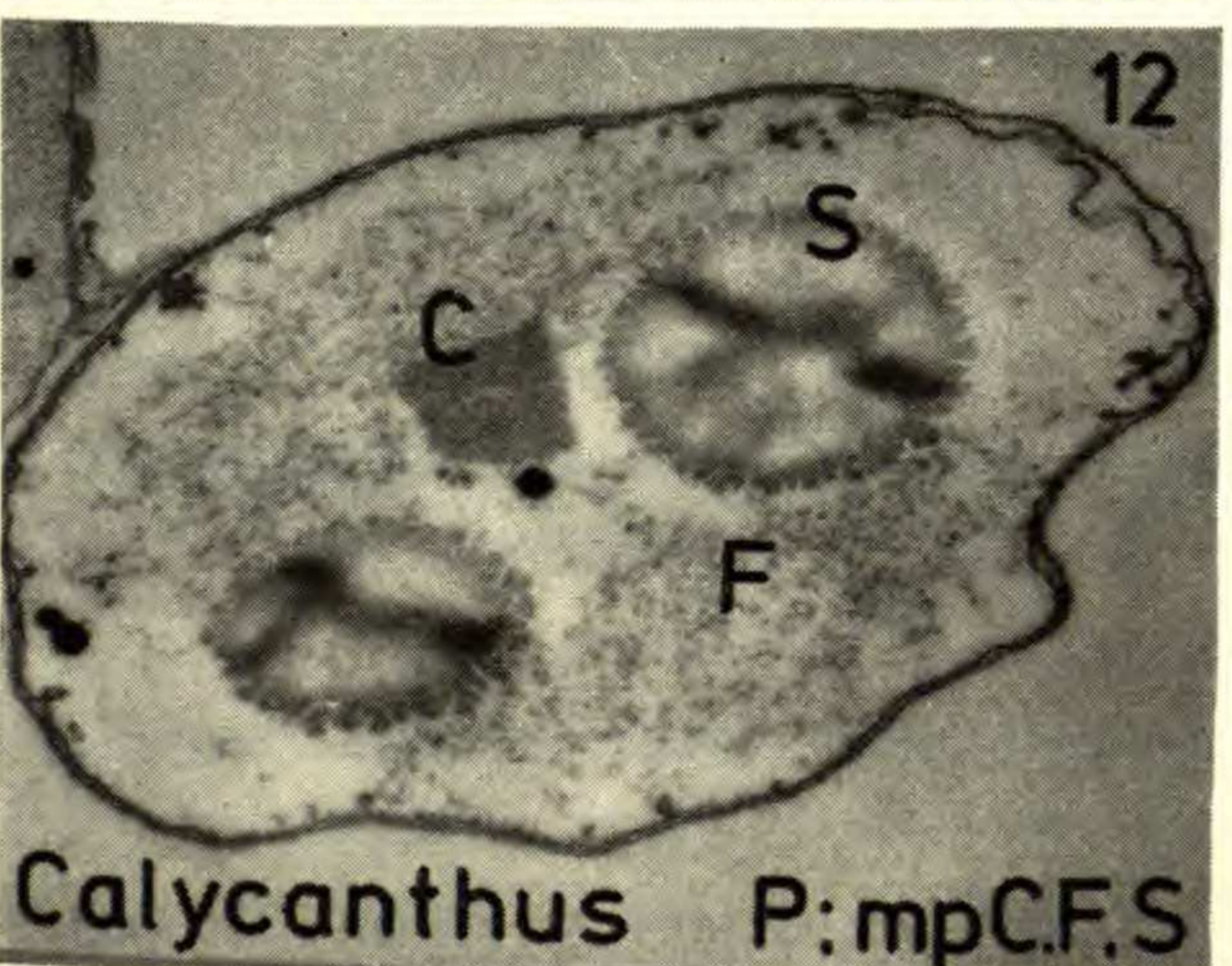
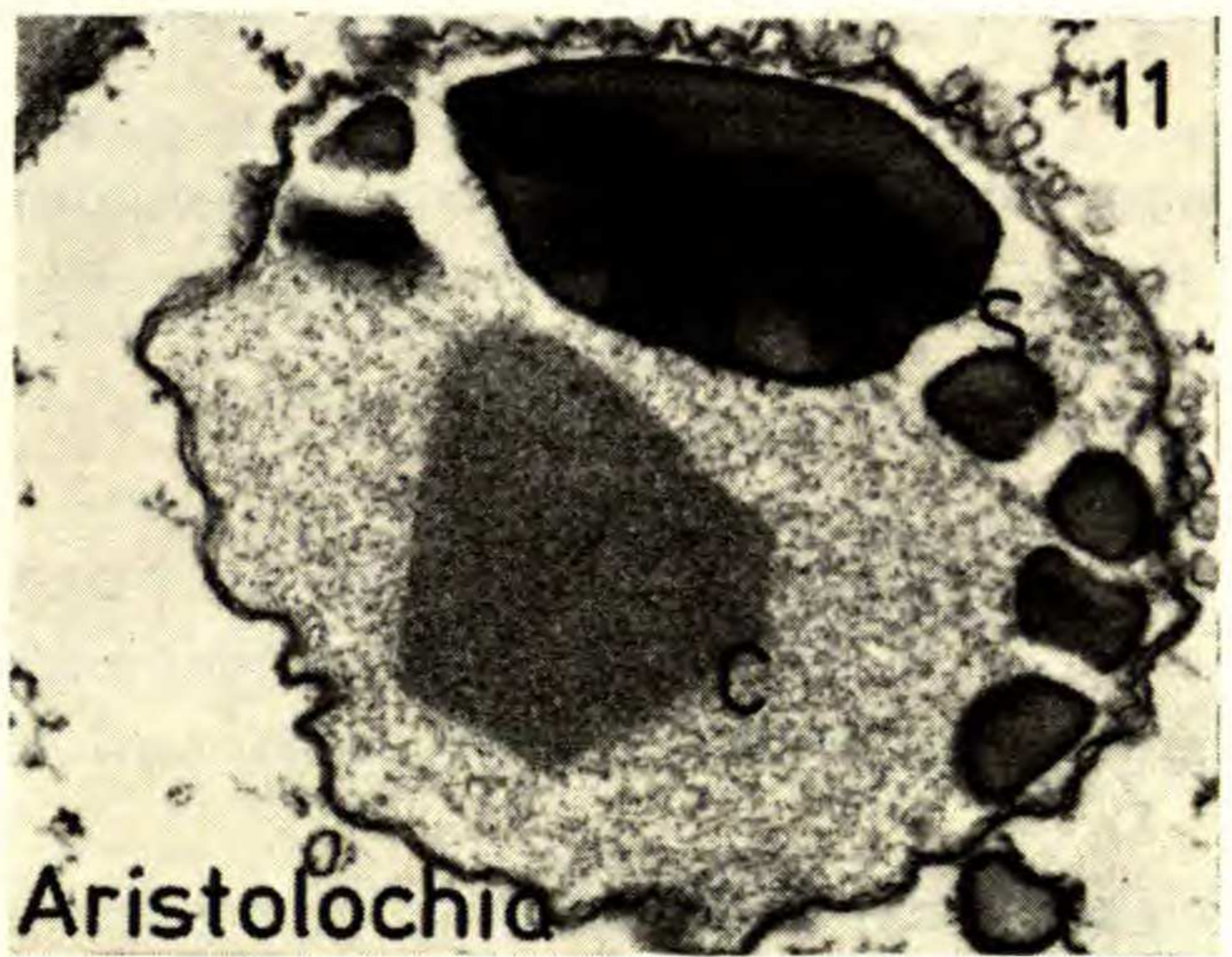
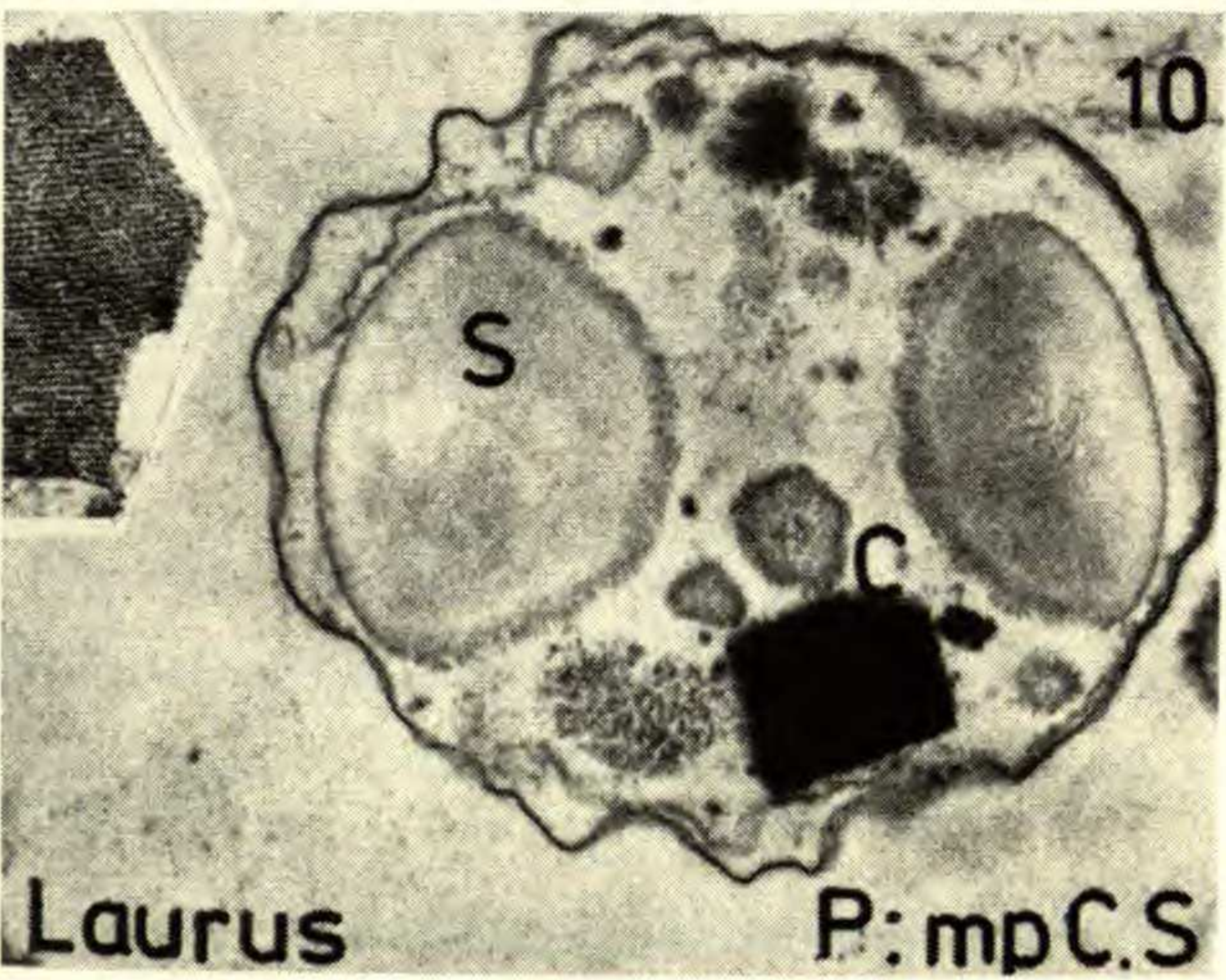
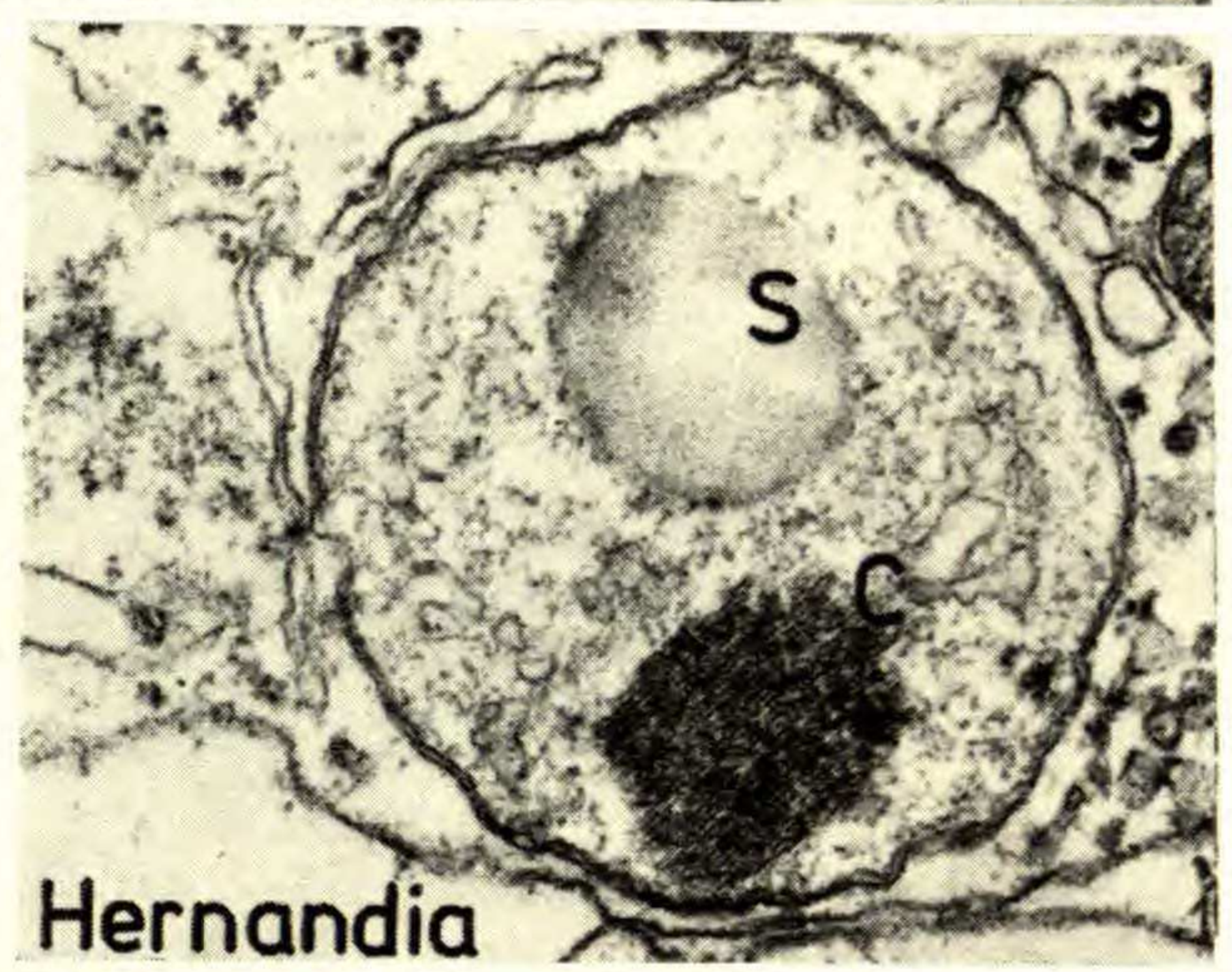
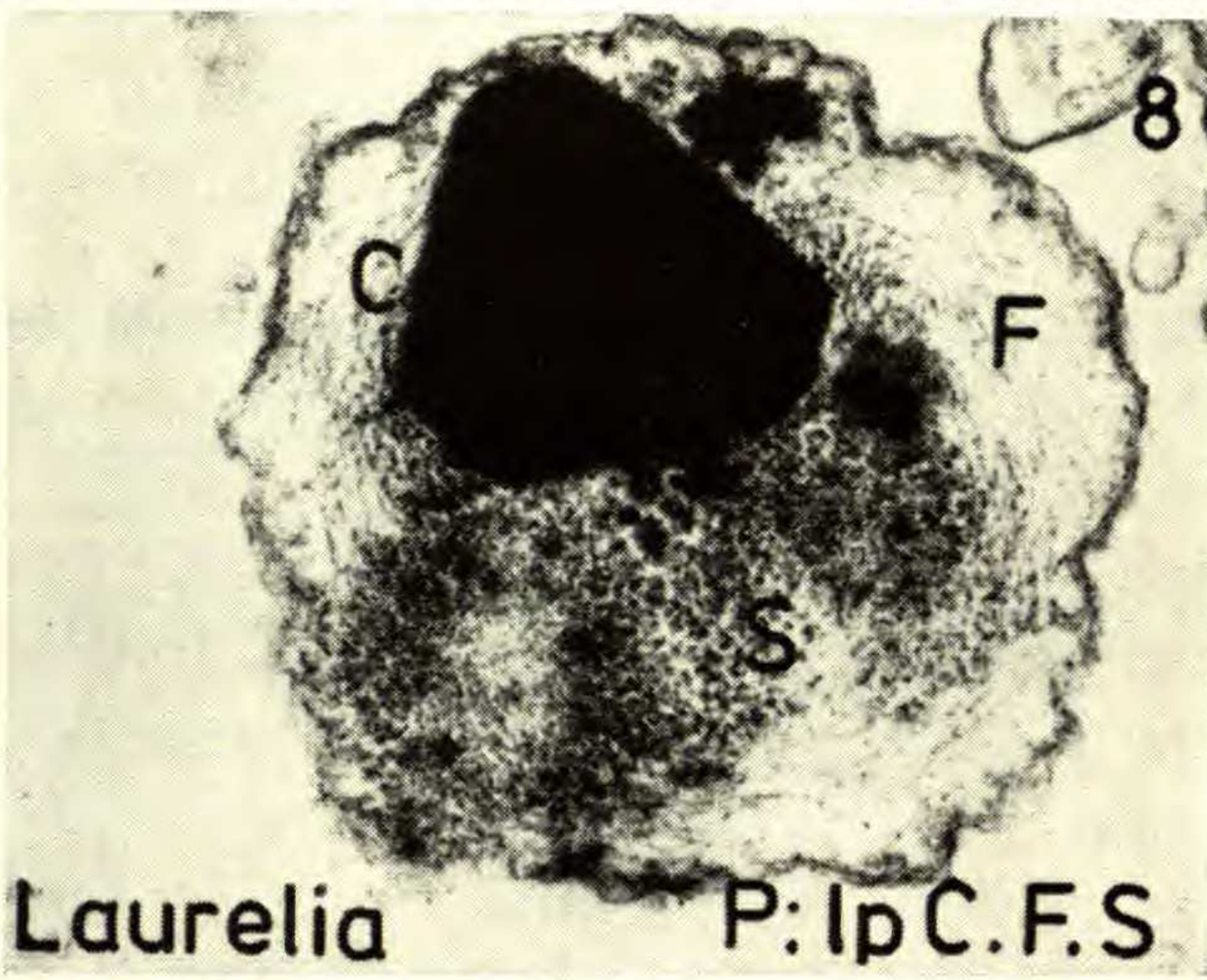
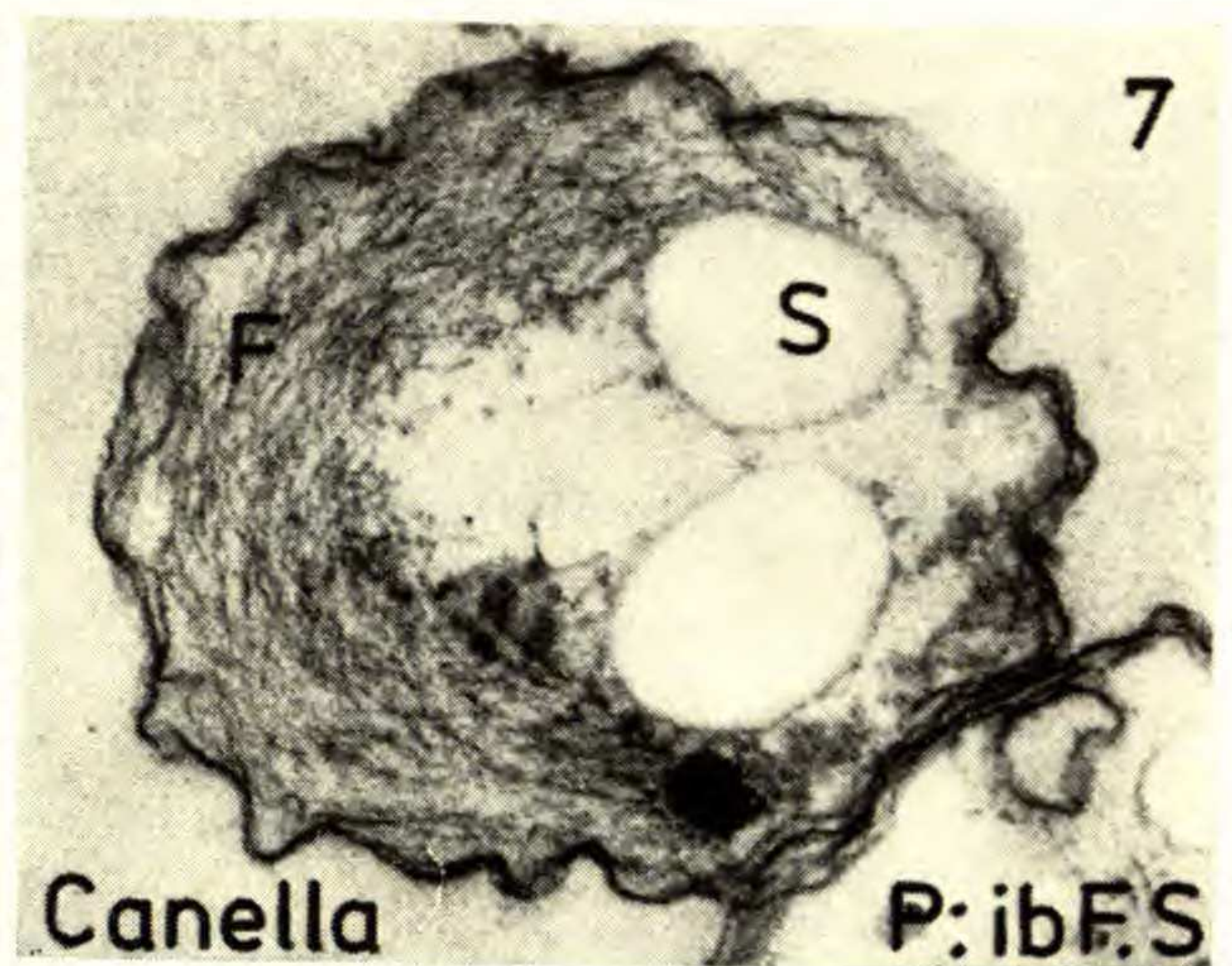
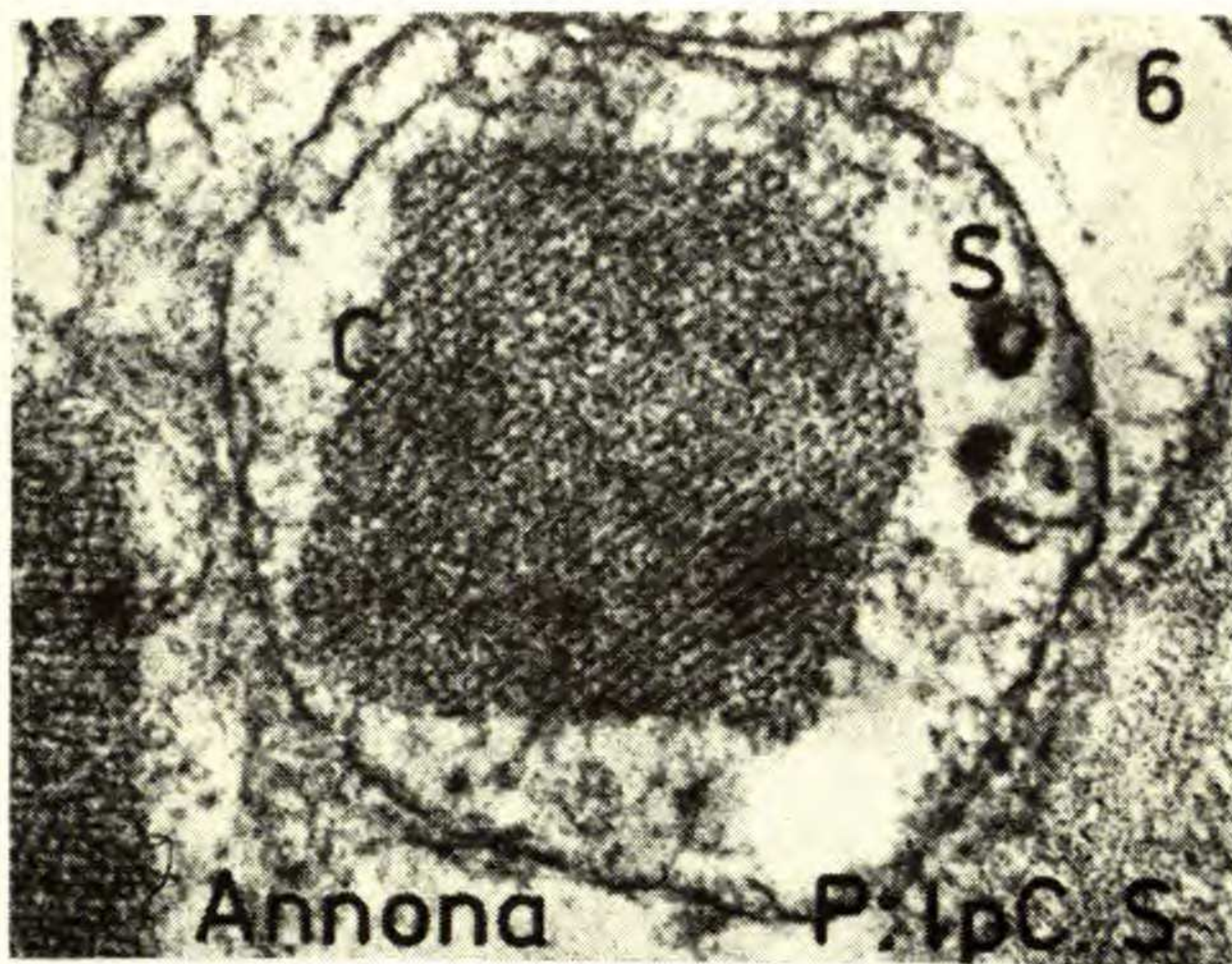


TABLE 3. S-type sieve-element plastids in Ranunculidae.^a (Figures following the families represent the number of investigated genera/species.)

Order 7: Illiciales		Glaucidiaceae	1/1
Illiciaceae	1/1	Hydrastidaceae	1/1
Schisandraceae	2/2	Nandinaceae	1/1
		Berberidaceae	5/5
Order 8: Nelumbonales		Order 10: Papaverales	
Nelumbonaceae	1/1	Papaveraceae	1/1
Order 9: Ranunculales		Fumariaceae	1/1
Lardizabalaceae	3/3	Order 11: Sarraceniales	
Menispermaceae	4/6	Sarraceniaceae	1/1
Ranunculaceae	4/5		
TOTALS 26/29			

^a All investigations by the author, except for *Eranthis hiemalis* (Pacini & Cresti, 1972).

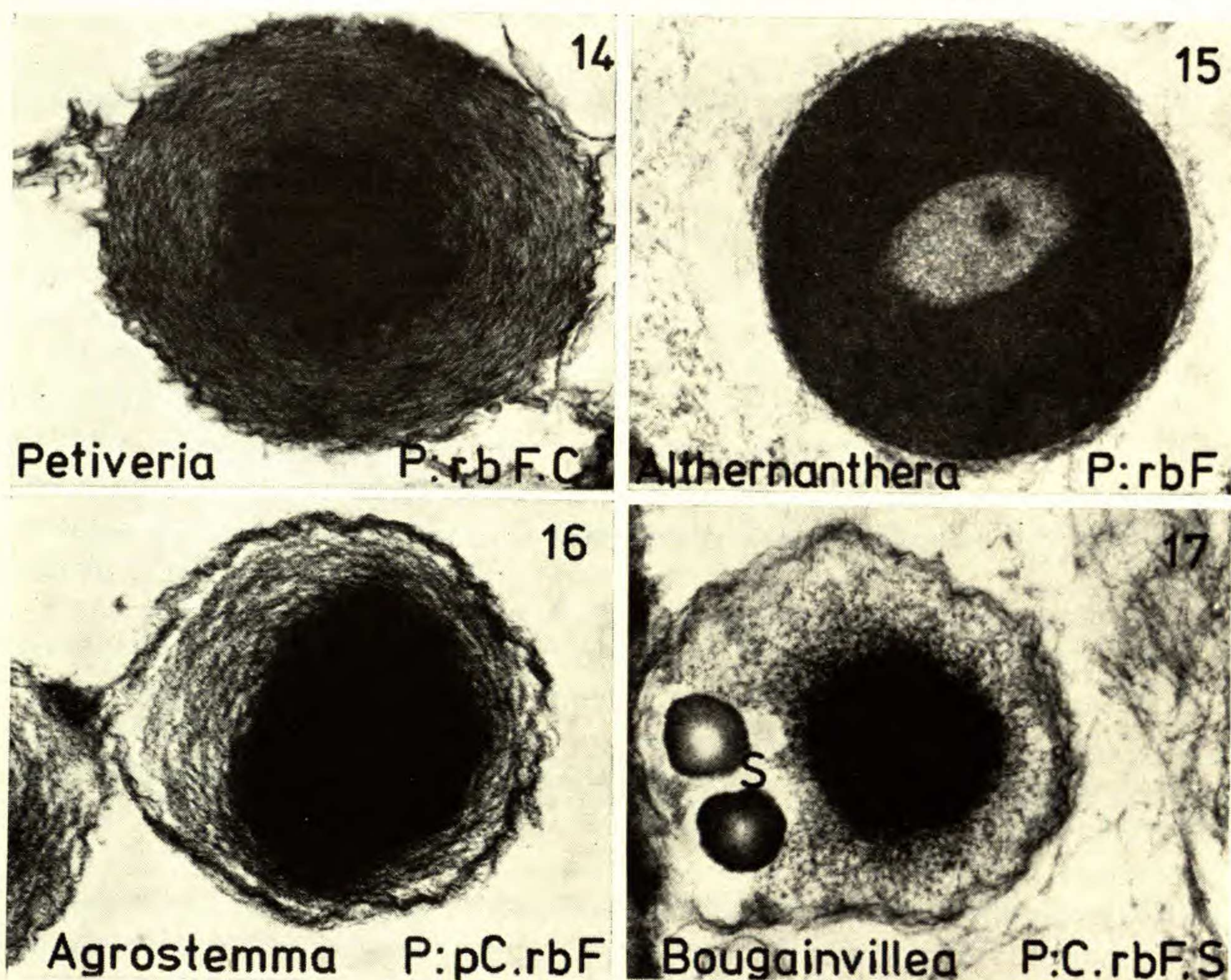
for this subclass (Table 3). However, as discussed previously, there is a limitation in the application of the ultrastructure of S-type sieve-element plastids to taxonomic problems below the subclass level in Ranunculidae.

Hamamelididae.—This subclass, which according to ultrastructural data presented in Table 4 has a rather uniform distribution of S-type plastids, initially gave some problems in plastid classification during part of the studies performed (see Behnke, 1973). A number of species from Urticales, that had been reported in earlier light microscopic investigations to contain no plastids in their sieve-

TABLE 4. Sieve-element plastids in Hamamelididae.^a (Figures following the families represent the number of investigated genera/species; P = P-type, S = S-type plastids.)

Order 12: Trochodendrales		Order 19: Barbeyales	
Trochodendraceae	S 1/1	Barbeyaceae	S 1/1
Order 13: Cercidiphyllales		Order 20: Casuarinales	
Cercidiphyllaceae	S 1/1	Casuarinaceae	S 1/2
Order 14: Eupteleales		Order 21: Fagales	
Eupteleaceae	S 1/1	Fagaceae	S 3/3
Order 16: Hamamelidales		Order 22: Betulales	
Hamamelidaceae	S 4/4	Betulaceae	S 5/5
Altingiaceae	S 1/1	Order 24: Myricales	
Platanaceae	S 1/1	Myricaceae	S 1/1
Order 17: Eucommiales		Order 25: Juglandales	
Eucommiaceae	S 1/1	Juglandaceae	S 3/3
Order 18: Urticales		Order 26: Leitneriales	
Ulmaceae	S 2/4	Leitneriaceae	S 1/1
(<i>Ulmus</i>)	P 1/3		
Moraceae	S 5/6		
Cannabaceae	S 2/2		
Urticaceae	S 8/9		
TOTALS S 42/47; P 1/3			

^a All investigations by the author, except for *Ulmus americana* (Evert & Deshpande, 1969).



FIGURES 14–17. P-type sieve-element plastids of Caryophyllales; general subtype, P:g/pC.rbF.—14. Globular crystalloid.—15. Variation P:rbF; no crystalloids in Amaranthaceae and Chenopodiaceae.—16. Variation P:pC.rbF; central crystalloids polygonal in Caryophyllaceae.—17. Variation P:C.rbF.S; starch in addition to crystalloids and filaments (of minor taxonomic importance).

elements, displayed plastids during ultrastructural studies but turned out to lack any prominent storage product. Since a thorough investigation then revealed at least some starch in some of these species, they were classified as having S-type plastids (Behnke, 1973).

Only the genus *Ulmus* (3 species investigated) deviates from the general pattern of this subclass. First shown for *U. americana* by Evert & Deshpande (1969) and later affirmed for two more species by the author, this genus contains P-type plastids that elaborate distinct rhomboidal crystalloids. This feature is explained as the result of the independent origin of this character and is not related to its occurrence in other taxa.

Caryophyllidae.—Caryophyllidae are among those subclasses whose scope has been changed several times due to intense investigations of almost every character contributing to a taxonomic classification. Once a specific P-type plastid in the sieve-elements of a couple of species was observed (Behnke, 1969b), efforts were made in ultrastructural studies to cover the entire group including all of its different families (Behnke & Turner, 1971; Behnke, 1972, 1974b, unpublished data). Investigated were 130 species of 16 of the 17 families listed by Takhtajan

TABLE 5. Sieve-element plastids in Caryophyllidae.^a (Figures following families represent the number of investigated genera/species.)

Sieve-element plastid types			
P-type		S-type	
Order 27: Caryophyllales		Order 27: Caryophyllales	
Phytolaccaceae	11/15	Gyrostemonaceae	1/1
Nyctaginaceae	3/6	Bataceae	1/1
Molluginaceae	2/3	Order 28: Polygonales	
Aizoaceae	11/12	Polygonaceae	2/3
Tetragoniaceae	1/2	Order 29: Plumbaginales	
Cactaceae	8/10	Plumbaginaceae	3/4
Portulacaceae	10/19		
Basellaceae	2/2		
Didiereaceae	4/6		
Halophytaceae	1/1		
Hectorellaceae	1/1		
Caryophyllaceae	16/20		
Amaranthaceae	11/16		
Chenopodiaceae	12/15		
TOTALS P 93/128		TOTALS S 7/9	

^a All investigations by the author except for *Tetragonia expansa* (Falk, 1964), *Beta vulgaris* (Esau, 1965), *Polygonum fagopyrum* (Arsanto, 1970), *Echinomastus intertextus* (Riviera, personal communication), *Opuntia subulata* (Delay & Darmanaden, 1973).

(1973) under the order Caryophyllales (see Table 5), and all of the families placed by Cronquist (1968) within the same order. Except for two families, all contained specific P-type plastids (P:rbF. [C.S]) characterized by peripheral ring-shaped bundles of protein filaments (Figs. 14–17) and often encircling an additional crystalloid. This list includes all of those families that were shown to contain betalains (Mabry et al., 1972; Mabry, this symposium); genera that are sometimes segregated as families: Achatocarpaceae, Agdestidaceae, Petiveriaceae, Stegnospermaceae, Dysphaniaceae; and two anthocyanin-containing families: Caryophyllaceae (including Illecebraceae) and Molluginaceae.

There are some structural modifications within the Caryophyllales subtype of P-type plastids which distinguish some families: Chenopodiaceae and Amaranthaceae lack the central crystalloid (Behnke, 1974b). Their plastid subtype is P:rbF (Fig. 15). Caryophyllaceae can be distinguished from the other families by their polygonal crystalloid (Fig. 16: subtype P:pC.rbF). A more detailed description of family characteristics among Caryophyllales and their interrelationships is being prepared (Behnke, 1976a).

The plastid investigations once more gave strong evidence for the inclusion of the Cactaceae and Didiereaceae in the Caryophyllales, as was earlier indicated by morphological and phytochemical work (Rauh & Reznik, 1961; Mabry et al., 1963). From the same kind of investigations, however, evidence should be drawn to exclude Bataceae and Gyrostemonaceae from the Caryophyllales. These are the only families of Caryophyllales, sensu Takhtajan, that have S-type plastids (Behnke & Turner, 1971; Behnke, unpublished observations). Bataceae contain neither betalains nor anthocyanins (Mabry & Turner, 1964); in Gyrostemonaceae pigmented parts have not been found yet. Pollen morphology in Gyrostemonaceae

and Bataceae is unique and strictly different from Phytolaccaceae or other Caryophyllales (cf. Eckardt, 1964; Nowicke, 1975). This may be regarded as another point in favor of a separation of these families from the order Caryophyllales.

Cronquist (1968) raises Bataceae to the rank of a separate order Batales which he arranges with the S-type containing orders Polygonales and Plumbaginales following the order Caryophyllales. From the ultrastructural data on sieve-element plastids this alliance could be favored against Takhtajan's treatment, since it associates nearly all S-type containing taxa of the subclass Caryophyllidae.

Whether Bataceae should be moved to the Capparales as suggested by Schraudolf et al. (1972) based on the presence of myrosin, or kept among Caryophyllidae, should be decided by further investigations. Viewed from evidence of sieve-element plastid investigations, their alliance to Capparales would not be excluded. Species of this order have also been recorded to contain S-type plastids (Behnke, 1972).

Many genera that by some systematists were allied with Caryophyllidae (or Centrospermae) were also found to contain S-type sieve-element plastids:

(1) *Theligonum* was formerly treated as separate order following Plumbaginales. Recently anthocyanins have been detected in this genus (Mabry et al., 1975). Strong evidence is accumulating from other phytochemical (Kooiman, 1971), as well as morphological and embryological (Wunderlich, 1971), investigations which indicates that Theligonaceae should be closely related to Rubiaceae. Sieve-element plastid investigations in this family demonstrated S-type plastids throughout (Behnke, 1975b).

(2) *Fouquieria* and (3) *Frankenia*, both belonging to Tamaricales and previously doubtfully allied to Centrospermae, contain S-type plastids (Behnke, 1976b).

(4) *Rhabdodendron*, associated to Centrospermae by Prance (1968), develops P-type plastids of a subtype not comparable to the Caryophyllales-type (Behnke, 1976b).

(5) *Viviania*, claimed by Bortenschlager (1967) to have pollen grains whose pollen morphology is like that of Phytolaccaceae, and listed as a separate family among Caryophyllales by Takhtajan (1973), was not available for ultrastructural studies of sieve-element plastids.

CONCLUDING REMARKS ON PHYLOGENY OF MAGNOLIOPHYTA AS DERIVED FROM ULTRASTRUCTURE OF SIEVE-ELEMENT PLASTIDS

Apart from the statement that there are some taxa with a fairly well restricted and specific plastid type, there are different possibilities of interpretation of how the present distribution of types of sieve-element plastids (Fig. 18) can be related to the phylogeny of Magnoliophyta. One interpretation is that all of the different patterns (S- as well as P-types) have an independent origin, an assumption that has been proven valuable for some other characters. We presently are inclined to follow another interpretation which presupposes a common origin of all of the plastid types. But as yet, we do not know what kind of common origin, that is, neither which plastid type arose first nor in which taxonomic group it arose. Our hypothesis is that accumulation of only one product—either starch or protein—is

THE DISTRIBUTION OF P-TYPE AND S-TYPE SIEVE-ELEMENT PLASTIDS IN SPERMATOPHYTES

Subclasses of MAGNOLIOPHYTINA arranged after TAKHTAJAN (1973), the size of the circles is proportional to the number of species, recounted from ENGLER's Syllabus

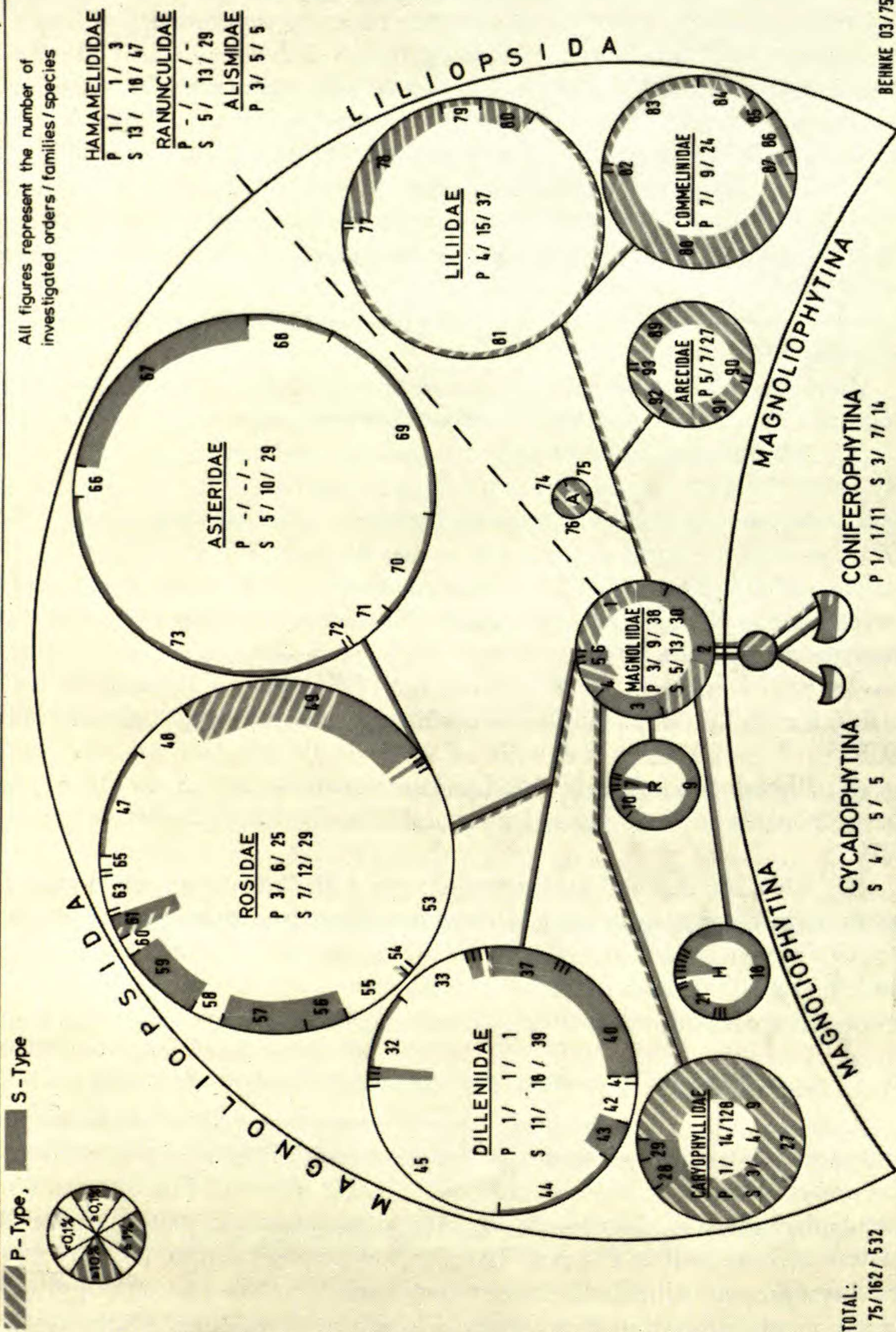


TABLE 6. Sieve-element plastids of Gymnospermae.^a (Systematic arrangement after Ehrendorfer, 1971; figures following the families represent the number of investigated genera/species; P = P-type, S = S-type plastids.)

Coniferophytina		Cycadophytina	
1. Ginkgoatae		2. Cycadatae	
Ginkgoaceae	S 1/1	Cycadaceae	S 1/1
2. Pinatae		Zamiaceae	S 1/1
Araucariaceae	S 1/1		
Pinaceae	P 7/11	4. Gnetatae	
Taxodiaceae	S 4/4	Ephedraceae	S 1/1
Cupressaceae	S 4/4	Welwitschiaceae	S 1/1
Podocarpaceae	S 2/2	Gnetaceae	S 1/1
Cephalotaxaceae	S 1/1		
3. Taxidae			
Taxaceae	S 1/1		
TOTALS P 7/11; S 19/19			

^a For references see Behnke (1974a).

first, that the capacity to accumulate the other product is gained later, and that the synthetic activity for the original product is sometimes lost. Starch is the most common accumulation product in sieve-elements of lower vascular plants (Evert, personal communication) and Gymnospermae (Table 6) and this favors the S-type plastid as being the primitive one. In contrast to this, the reappearance of starch among P-type plants of some of the advanced orders of Liliopsida may provide evidence for the pure P-type plastid as being the primitive one. So far this can not be decided. The common origin, if any, should probably be sought in the groups traditionally thought to be closely related to angiosperm ancestors. But, if we adhere to a common line within the recent Magnoliophyta—independent of what was first, starch or protein—Caryophyllales can not easily be derived from the Ranunculales as proposed by Takhtajan (1973). Unless we suppose a second independent origin of Caryophyllales P-type plastids, they should be traced back directly to Magnoliidae or their ancestors. The latter is more likely since in Pinaceae (Table 6) there are P-type plastids (P:g/pC.rbF.S) that are very similar to the type of plastids in Caryophyllales.

The schematic representation of the distribution of types of sieve-element plastids among the subclasses of Magnoliophyta (investigated species expressed in percentage of recorded species) and the probable interrelationships between the plastid types as expressed in Fig. 18 follows only one line of interpretation and investigation. There are important arguments for the independent origin of the plastid types within different taxa. Further investigation in this field is hopefully expected to provide stronger evidence for one hypothesis or the other.

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FIGURE 18. P- and S-type sieve elements in seed plants. Distribution of investigated species is given as a percentage of the total number of species by the shaded areas within the subclass circles (see percentage explanation in upper left circle). Peripheral figures within circles represent the numbering of orders after Takhtajan (1973).

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